

COEXISTENCE IN TWO SPECIES OF *HOLCOCEPHALA*
(DIPTERA: ASILIDAE) IN A MARYLAND
HABITAT: PREDATORY BEHAVIOR

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Abstract.—Coexistence was studied in two species of *Holcocephala* in a Maryland habitat. General behavior patterns of *H. abdominalis* (Say) and *H. calva* (Loew) were similar although each species exhibited significant variations. Coexistence is possible because the species differed in their selection of prey and foraging and feeding patterns.

The three Nearctic species of *Holcocephala*, *abdominalis* (Say), *calva* (Loew), and *fusca* Bromley, are usually found in mesic habitats and range from the eastern United States west to eastern Texas, Kansas, and Nebraska (Martin and Wilcox, 1965). They typically forage from tips of dead twigs or leaves of rank vegetation, located near or along margins of streams, fields, and woods (Baker and Fischer, 1975; Brimley, 1922; Bromley, 1931, 1946, 1950a, b; McAtee and Banks, 1970; Hull, 1962; Scarbrough, 1974; Johnson, 1976; Dennis, 1979). They sometimes forage from edges of wooded areas where vegetation patterns change abruptly, e.g. clearings, trails, and streams, but typically avoid dark thickly vegetated areas of forest (Scarbrough, 1974; Dennis, 1979). *Holcocephala abdominalis* is sometimes found foraging in dry fields, a short distance from streams (Scarbrough, 1974) and forest margins (Johnson, 1976), especially when the fly is abundant. *Holcocephala calva* and *H. fusca* appear to restrict selection of perches to vegetation along tree lined margins of trails, footpaths, lawns, and streams (Scarbrough, 1974; Dennis, 1979).

Holcocephala abdominalis and *H. calva* are sometimes found within a common habitat, with the former species being apparently more abundant (Baker and Fischer, 1975; Bromley, 1931; McAtee and Banks, 1920). Dennis (1979) suggested that differences in population densities of the two coexisting species may result from interspecific competition. Coexistence between interacting populations occurs when the species involved exploit resources differentially, with their realized niches being dissimilar in at least one im-

portant dimension (MacArthur, 1958; DeBach, 1966). If this principle is operable then it can be assumed that one or both *Holcocephala* species have adjusted, e.g. partitioned resources, in such a way as to reduce competition by more effectively exploiting the available resources. The purpose of this study was to examine coexistence of *H. abdominalis* and *H. calva* in a Maryland habitat in terms of resource partitioning involving foraging behavior, prey selection, and predation between the two species.

HABITAT AND METHODS

This study was conducted in a mesic hardwood picnic area, located near York Road in the northeast section of the Towson State University campus, during July, August, and September of 1973 through 1977. The linear 2.2 ha plot has steep margins, which drop 8 to 10 m in elevation from the surrounding campus, and is traversed by a stream and several footpaths. Woody vegetation in the study area consisted of a mixed stand of bottom land trees, with *Liriodendron tulipifera* L., *Platanus occidentalis* L., *Quercus* spp., *Prunus serotina* Ehrh., and *Gleditsia triacanthos* L. along the sloped margins; and with *Juglans nigra* L. and scattered *Ulmus americana* L., *Fagus grandifolia* Ehrh., *Acer* spp., and *Pinus* spp. predominating on the flat. This overstory produced a continuous shaded condition during the day, except for brief periods in the middle of the day and late afternoon. A dense shrub growth of *Vitis* sp., *Rubus* sp., *Lonicera* sp., *Lindera benzoin* Blume, and herbaceous plants occurred along the steep slopes, stream and less disturbed areas. Temperatures and relative humidities ranged from 14°C and 99% in early morning to 36°C and 28% in mid-afternoon.

Prey selection and predation by the two species was determined via surveying flies along a standard route of ca. 100 m and following individual flies for 1–2 h periods. These techniques were necessary in order to identify the timing of major behavior patterns and for subsequent analysis of individual patterns. Prey samples were taken hourly per day during the survey and later measured for total body length (Scarborough and Sraver, 1979). Further information on types and selection of prey was taken while individuals were under surveillance, although prey were not taken. Surveillance of flies was made under bright skies from 0600 to 2000 h (EST) during 1974 and 1975. Flies were selected randomly for surveillance (see Scarborough and Norden, 1977), marked on their thoracic notum with fast drying enamel paint and released. They were then followed to a perch where a 15 min interval elapsed before data was taken. As indicated above, most flies were observed for two consecutive hours during which time their complete behavioral repertoire was recorded. Males, however, were sometimes difficult to follow when they were actively searching for mates. Consequently males were followed for only one hour. At the end of each observation period,

additional flies were selected and followed for the subsequent period. Data, resulting from the observation of adults of each species, were then compiled to form a theoretical 14 h ten-day period. A combined total of 140 females and 198 males were monitored. Temperatures and relative humidities were taken approximately 1.5 m above ground level and adjacent to each perched fly each observation hour.

RESULTS AND DISCUSSION

Foraging behavior.—Data generated by this study showed that the general foraging behavior of the two *Holcocephala* species was similar, and essentially agreed with that reported in earlier studies (Dennis, 1979; Johnson, 1976). Both species usually foraged from shaded vegetation along tree line margins of the study site, utilizing perches between 0.2 and 5.0 m above ground level. However, *H. abdominalis* differed in that it was invariably more abundant and foraged from perches on low vegetation (<1.0 m), whereas *H. calva* was more abundant and foraged from perches on taller vegetation (>1.5 m). *Holcocephala abdominalis* also differed from *H. calva* in that as its population density increased in late August, it dispersed into the open, dry sunlit clearings and foraged from flower spikes and leaf tips of *Plantago lanceolata* L. and other herbaceous vegetation (0.2 to 0.4 m). These results agree with other reports (Scarborough, 1974; Johnson, 1976) wherein *H. abdominalis* has been found resting on and foraging from weedy vegetation in dry fields which border streams and wooded areas. Dispersion to adjacent areas is apparently initiated by increased interactions between increased densities of conspecifics and congenics for limited perches (unpublished data). *Holcocephala calva*, like *H. fusca* (Dennis, 1979), was rarely found utilizing perches away from the edges of these clearings, but usually rested on and foraged from perches in the aforementioned locations.

Asilids, except those of the Leptogasterinae, typically forage under brightly lit conditions. *Holcocephala fusca* in Virginia (Dennis, 1979) and *H. abdominalis* in Indiana (Johnson, 1976) behave similarly in that they usually foraged and captured prey in open sunlit areas. In an earlier study, I found several specimens (>300) of *H. abdominalis* foraging from sunlit weedy vegetation throughout an abandoned pasture (20,235 m²) at Allerton Park, Ill. (unpublished data). However, at the Towson study site and others in Maryland, neither species consistently foraged nor captured prey in direct sunlight. Both species usually foraged from shaded sites and captured prey which were "back lighted" against a bright sky, often without venturing into direct sunlight. The exception to the latter occurred in late afternoons when forage sites were sunlit for short periods and temperatures were high (Fig. 1). These sites were also sunlit for short periods in early morning, but temperatures and foraging activities were correspondingly low. *Holcoceph-*

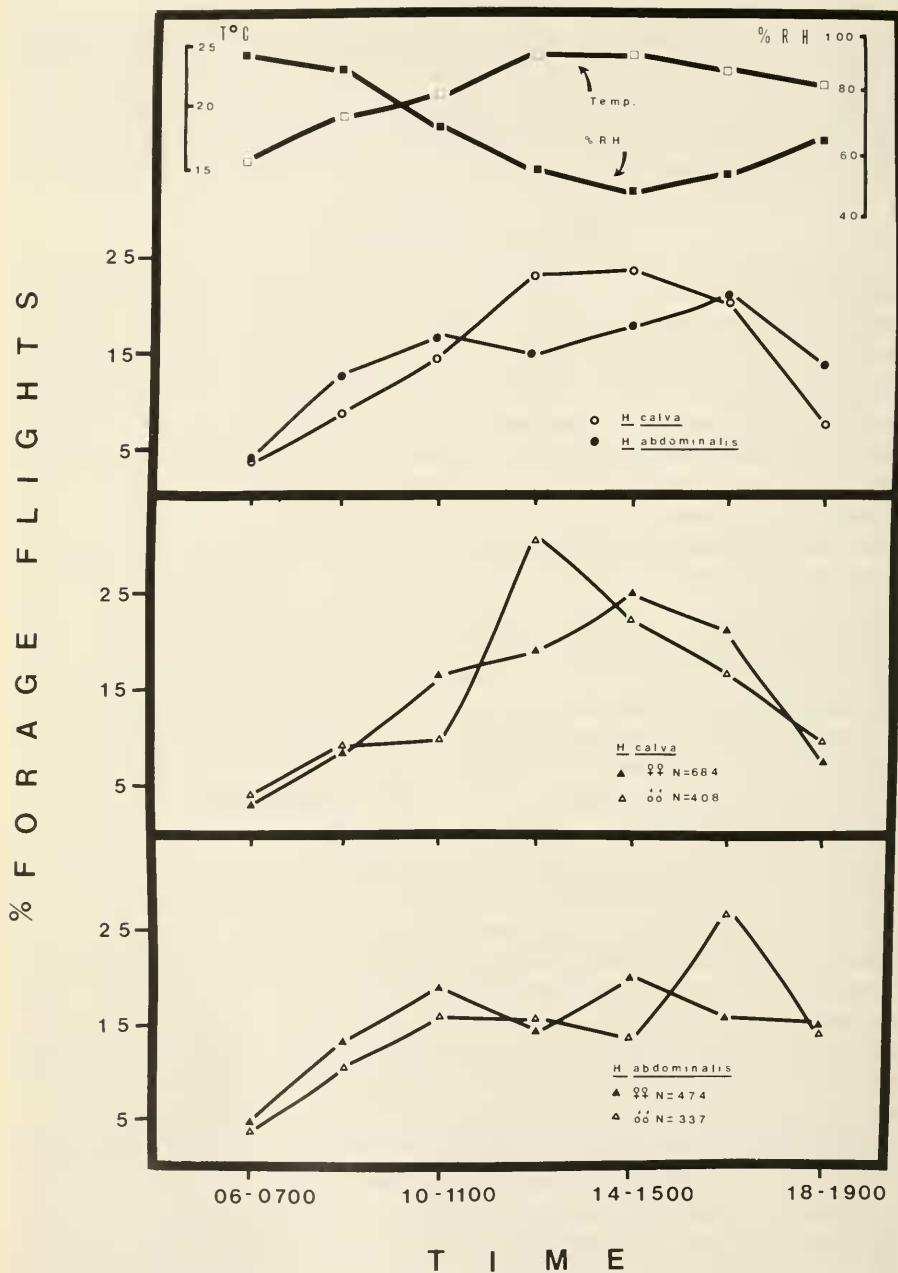


Fig. 1. Comparisons of intra- and interspecific foraging behavior per two hour period during a 14 h day for two species of *Holcocephala* in Maryland.

ala abdominalis differed from *H. calva* in that its foraging sites were sunlit more often and for longer periods and, hence, it foraged more frequently under sunlit conditions.

Length of forage flights of the two species varied ($R = 3\text{--}150$ cm), although most prey (90.5%) were captured between 15 to 100 cm from the forage site. *Holcocephala abdominalis* captured most prey (88.2%) between 20 and 60 cm of the forage site, whereas *H. calva* captured most prey (92.1%) between 40 and 100 cm. As reported in other studies of *Holcocephala* (Dennis, 1979; Johnson, 1976), prey were captured in air either in front of the forage site or to one side of it, with the predator usually returning to the same forage site. Both species foraged in an oblique path, with the greatest rise occurring near the interception point. Thus, prey were invariably captured above the forage site. Upon capturing the prey, the predator's flight path looped above, and sometimes behind the previous perch where it came to rest. If the interception point was far to one side of the forage site, the fly did not always compensate in the return flight, missing the previous perch but landing at a nearby site. The latter usually occurred when prey were large (>3 mm) or the distance to the prey was unusually long (>100 cm).

Figure 2 shows foraging patterns of *Holcocephala* expressed as proportions of total flights. Foraging activities between species ($\chi^2 = 75.1$, $P < .001$) were significantly different, with each species showing characteristic foraging patterns. Both species foraged during each observation period, with the lowest proportion of flights occurring during the first and last periods of the day. The foraging pattern of *H. calva* peaked during the early afternoon, but had decreased significantly by the last observation period. In contrast, the peak foraging period of *H. abdominalis* was short and occurred in late afternoon, following a consistent but lower level of foraging. The latter species also exhibited a significant decrease in foraging by late afternoon, but the decrease was less than that for *H. calva*. Furthermore, a greater proportion of the foraging flights were made earlier in the day ($Z^1 = 3.08$, $P < .05$) by *H. abdominalis* than *H. calva*, producing a slightly greater rapid rise in foraging activities.

Foraging patterns of conspecifics ($\chi^2 = 17.6$, $P < .01$, *H. a.*; $\chi^2 = 35.6$, $P < .001$, *H. c.*) and congeners ($\chi^2 = 33.1$, $P < .001$, ♂; $\chi^2 = 42.1$, $P < .001$, ♀) also differed significantly (Fig. 1). Males of both species showed abrupt, rapid increases in foraging flights which exceeded that for conspecific females. However, the peaks produced by male activity differed in time and duration from that of *H. calva*, occurring earlier in the day, but extending for longer periods in late afternoon. Female *H. calva* foraged

¹ Differences between proportions (Z) from Zar (1974).

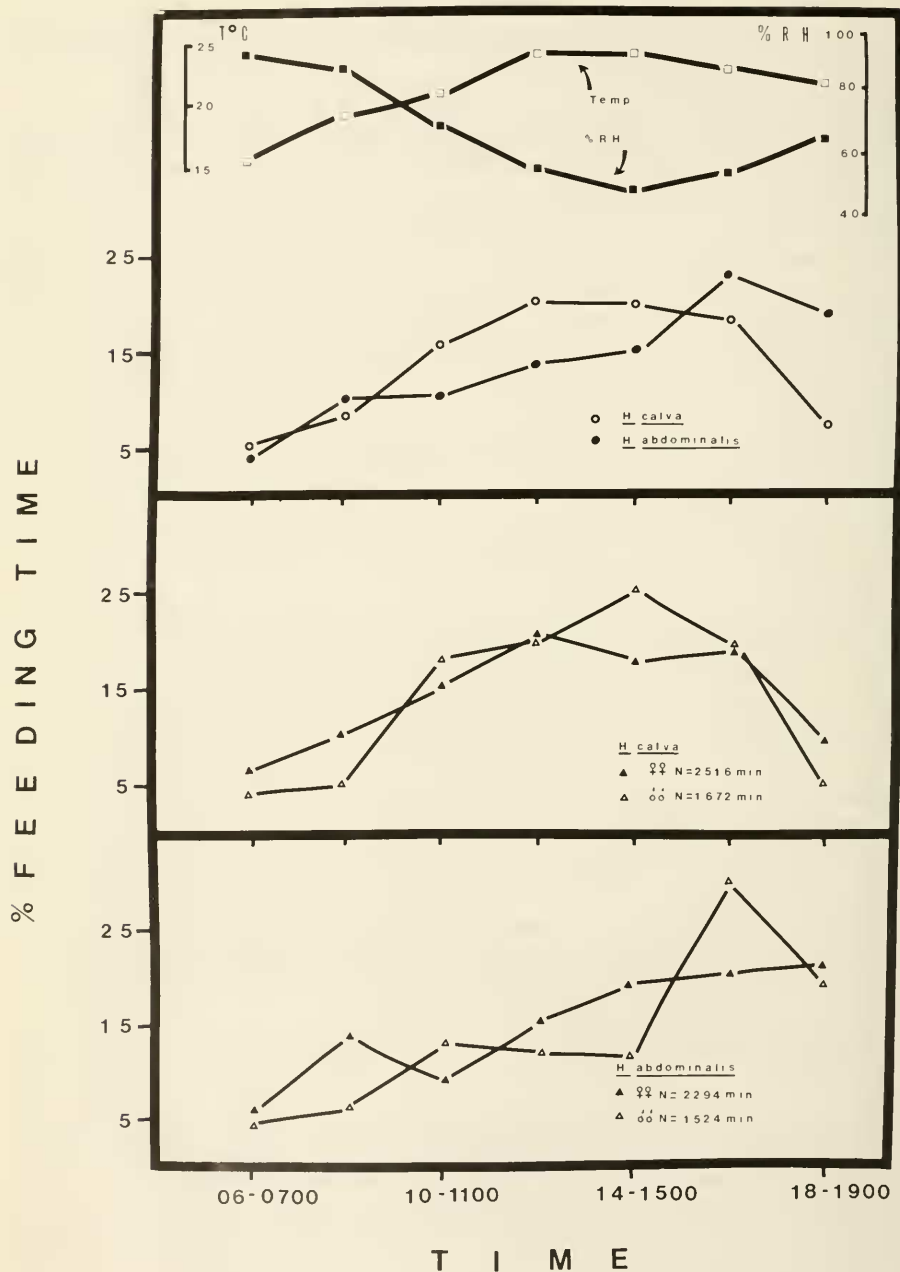


Fig. 2. Comparisons of intra- and interspecific feeding behavior per two hour period during a 14 h day for two species of *Holcocephala* in Maryland.

Table 1. Foraging responses of two species of *Holcocephala* toward potential prey. Data for conspecific males and females within a column are not significantly different. Data between congeneric sexes or totals for species within a column are significantly different at $P < .01$ level.

Species	Captured		Non-Captured		Investigated	
	No.	%	No.	%	No.	%
<i>H. abdominalis</i>	350	43.9	26	3.3	421	52.8
Males	142	42.1	13	3.9	182	54.0
Females	208	45.2	13	2.8	239	52.0
<i>H. calva</i>	452	37.7	25	2.1	721	60.2
Males	179	37.9	5	1.0	294	61.5
Females	273	37.7	20	2.8	427	59.3

more frequently in mid- to late afternoon following a steady increase during the earlier part of the day. In contrast, female *H. abdominalis* showed an increase in foraging until 1000 h, after which no significant change occurred.

When potential prey flew near specimens of either perched species, their movements usually stimulated them to chase. Upon approaching the potential prey in flight, the asilids either rejected the prey item without physical contact or attempted to capture it. Table 1 shows the responses of *Holcocephala* to potential prey. Foraging responses between conspecific males and females were similar ($\chi^2 = 1.21$, $P < .05$, *H. a.*; $\chi^2 = 3.14$, $P < .05$, *H. c.*), whereas significant differences ($\chi^2 = 11.63$, $P < .01$) existed between species. *Holcocephala abdominalis* successfully captured ($\chi^2 = 7.93$, $P < .01$) a greater proportion of prey, but investigated ($\chi^2 = 10.59$, $P < .01$) fewer potential prey than did *H. calva*. Both species immobilized most prey that they captured. Some large prey were released or dropped without being immobilized during the return flight to the forage perch. These data suggest that perched *H. abdominalis* may be more capable of recognizing capturable potential prey than *H. calva*.

Feeding behavior. —Prey were usually impaled upon the hypopharynx of the predator at the time of capture, although large prey (>3.4 mm, e.g., *Reticulitermes flavipes* (Kollar) and *Ponera pennsylvanica* Buckley) were manipulated with all six tarsi near the forage site before insertion. The hypopharynx was usually inserted in the dorsum of the prey, normally in the thorax. The eyes and tip of the abdomen were sometimes used when prey were small (<2 mm) or following manipulation and after the asilid had been feeding for extended periods. Apparently the choice of the site for hypopharynx insertion was related to the manner in which the predator captured its prey. Both asilids usually captured prey by grasping the margin of the thorax, resulting in the largest part of the prey's body being directly below the predator's head.

Additional activities exhibited by both species while feeding included grooming, head movements, and manipulating prey. Perched asilids may groom any part of their body at any time. However, while feeding, grooming was limited to rubbing the hindlegs together or over the surface of wings and abdomen. Grooming of the more anterior parts of the body usually followed feeding. Rapid head and body movements directed toward moving objects suggested that the asilids detected both crawling and flying insects and other arthropods in the vicinity of their perches. Prey were manipulated while the asilids perched or hovered near the feeding site. During manipulation, the position of the hypopharynx in the prey was adjusted, usually involving its removal and insertion at a different site. The flies removed prey from the hypopharynx by pushing it off with the foretarsi while perching, whereas all six legs were used during its removal and manipulation while hovering. Hovers ($\bar{x} = 10$ s, $R = 6-20$, $N = 66$, *H. c.*; $\bar{x} = 7$ s, $R = 4-17$, $N = 48$, *H. a.*) varied in length, with longer times being associated with larger prey. The asilids invariably returned to previous perches to resume feeding following manipulation. *Holcocephala calva*, in contrast to *H. abdominalis*, sometimes manipulated prey without removing it from the hypopharynx by using one tarsus to "spin" it on the hypopharynx, or adjusting the depth of the hypopharynx by pushing the prey against the perch. *Holcocephala fusca* (Dennis, 1979) also has been reported to hover and manipulate prey.

While perching or feeding, the asilids were sensitive to moving shadows that accompanied abrupt changes in air currents. Depending upon the strength of the stimulus, they responded by flying to another location or by moving their hindlegs in an alternating "kicking" motion. If the stimulus occurred often, they retreated (ca. 2-3 cm) from the tip of a twig and repeated the "kicking." If the stimulus was strong, such as that produced by an approaching predator (e.g., *Vespula* spp., conspecifics and Araneida), they invariably flew to a nearby perch. Flight was more frequent when the stimulus was generated in front of the perched asilids. Leg motion and retreating occurred more frequently than flight, especially when the stimulation originated behind the asilids. Speed of leg movement was highly variable, but was apparently related to air velocity. The asilids were induced to kick at different frequencies either by blowing air upon them via a hollow tube at different velocities or by waving a hand near them at different speeds. Leg movement usually increased with either increased air current velocity or increased frequency of waving.

Dennis (1979) and Johnson (1976) reported that *Holcocephala* removed prey by either pushing it off the hypopharynx with a foretarsus or withdrawing the hypopharynx while perched or flying, allowing the prey to drop. Both species in this study also used these methods to remove prey at the completion of feeding. Furthermore, when the latter method was used at a

Table 2. Mean feeding times per prey and mean number of prey fed upon per unit time for two species of *Holcocephala* during 10 observation days in Maryland.

Species	Sample	Time/prey (min)	Prey/h/d	Prey/d
<i>H. abdominalis</i>	430	8.58	1.5	21.5
Male	172	8.25	1.2 ^a	17.1 ^a
Female	258	8.91	1.8	25.8
<i>H. calva</i>	423	9.15	1.8	25.3
Male	148	8.80	1.3 ^a	18.4 ^a
Female	275	9.44	2.3	32.2

^a Means followed by the same letter within a column are not significantly different. Remaining data between congeneric sexes or species within a column are significantly different at $P < .05$ level (t test).

perch, the asilid's head was tilted forward approximately 90°, positioning the hypopharynx in an almost 180° vertical plain to the ground. This behavior apparently enhances the role of gravity in removing the prey.

Table 2 depicts the mean feeding time per prey and mean number of prey fed upon per unit time for ten observational days. These data show that *H. calva* fed for significantly longer periods per prey and fed upon larger numbers of prey per h and per day than *H. abdominalis*. Similar differences were found between sexes of each species, with females feeding for longer periods and upon larger numbers of prey than males. In contrast, males differed from females in that they fed upon approximately equal numbers of prey per unit time. Differences in mean feeding times and mean number of prey are attributed to greater predator-prey size relationships and greater energy demands between the sexes and the species.

Time utilized for feeding per 2 h period per day for both species of *Holcocephala* varied significantly ($\chi^2 = 152.4$, $P < .001$), although each exhibited a distinct feeding pattern (Fig. 2). Both species fed for shorter periods during early morning, but showed increased feeding times by mid-morning. *Holcocephala calva* fed for consistently longer periods (1000 to 1700 h, no significant difference per 2 h period) through most of the day, although a significant decrease ($Z = 5.28$, $P < .05$) occurred in late afternoon. In contrast, feeding times were less ($\chi^2 = 4.9$, $P < .05$) from 1000 to 1500 h for *H. abdominalis* than for *H. calva*, but were significantly greater ($\chi^2 = 69.1$, $P < .001$) from 1600 to 1900 h. Feeding times also decreased ($Z = 16.7$, $P < .001$) in late afternoon for *H. abdominalis* but the decrease was significantly less than that for *H. calva*.

Conspecific asilids displayed significant variations ($\chi^2 = 134.1$, $P < .001$ ♂ vs. ♀ *H. a.*; $\chi^2 = 105.4$, $P < .001$ ♂ vs. ♀ *H. c.*) in feeding proportions during certain periods of the day (Fig. 2). Conspecific males utilized less feeding time than conspecific females from 0600 to 1000 h, but feeding times

Table 3. Correlations between foraging and feeding behavior with two environmental parameters for two species of *Holcocephala*.

Species	Temperature		RH	
	Foraging	Feeding	Foraging	Feeding
<i>H. abdominalis</i>	0.912 ^a	0.746 ^b	-0.821 ^b	-0.848 ^b
<i>H. calva</i>	0.786 ^b	0.861 ^b	-0.827 ^b	-0.856 ^b

^a $P < .01$.^b $P < .05$.

increased significantly by the 10–1100 period. Feeding times of male *H. calva* increased until 1500 h when they began to decrease. In contrast, feeding times of male *H. abdominalis* did not change significantly between 10–1500 h, but were followed by a rapid rise by 16–1700 h and a subsequent rapid decrease by 1900 h. Feeding times of females of both species tended to level off with only minor fluctuations following the rise in early morning. Feeding times of female *H. calva* decreased rapidly by 1900 h whereas those of *H. abdominalis* remained relatively consistent with former periods.

Foraging and feeding patterns for both species were positively correlated with temperature and negatively correlated with relative humidity (Table 3). As air temperatures increased and relative humidities decreased, both foraging rates and feeding times increased (Figs. 1, 2). Both species utilized less time for feeding and foraged less during early morning when temperatures were lowest and relative humidities greatest. Also, *H. calva* showed a significant decrease in foraging rates and feeding times in afternoon as relative humidities increased. Activities remained relatively constant in

Table 4. Dietary composition and characteristics of prey captured by two species of *Holcocephala* in Maryland. Predator lengths (mm) *H. calva*, $\bar{x} = 7.25 \pm 0.58$; *H. abdominalis*, $\bar{x} = 5.81 \pm 0.64$.

Prey	<i>H. abdominalis</i>			<i>H. calva</i>		
	No.	%	\bar{x} SD	No.	%	\bar{x} SD
Diptera	235	35.8	1.58 \pm 0.65 ^a	184	31.1	1.97 \pm 0.756 ^a
Hymenoptera	223	34.0	2.36 \pm 0.87 ^b	170	28.7	2.36 \pm 1.19 ^b
Coleoptera	106	16.2	1.54 \pm 0.59 ^a	59	10.0	1.88 \pm 0.67 ^a
Homoptera, Hemiptera	45	6.8	1.47 \pm 0.49 ^a	89	15.0	1.80 \pm 0.77 ^a
Psocoptera	27	4.1	1.67 \pm 0.42 ^a	72	12.2	1.82 \pm 0.50 ^a
Misc.	20	3.0	1.74 \pm 0.40 ^b	18	3.0	1.89 \pm 0.47 ^b
	656	99.9	1.73 \pm 0.57	592	100.0	1.95 \pm 0.73

^a Significant difference within prey taxa between species at $P < .05$ level.^b No significant difference within prey taxa between species (t test).

Table 5. Dietary composition and characteristics of prey captured for *Holcocephala abdominalis* in Maryland. Predator lengths (mm) 5.63 ± 0.59 ♂, $N = 20$; 5.9 ± 0.69 ♀, $N = 20$. Means within common taxa are not significantly different (*t* test).

Prey	Females			Males		
	No.	%	\bar{x} SD	No.	%	\bar{x} SD
Diptera	121	35.6	1.59 ± 0.71	114	36.1	1.13 ± 0.70
Hymenoptera	118	34.7	2.44 ± 0.83	105	33.2	2.35 ± 0.86
Coleoptera	51	15.0	1.47 ± 0.56	55	17.4	1.50 ± 0.57
Homoptera, Hemiptera	27	7.9	1.52 ± 0.47	18	5.7	1.43 ± 0.50
Psocoptera	13	3.8	1.67 ± 0.53	14	4.4	1.58 ± 0.35
Misc.	10	2.9	1.74 ± 0.40	10	3.2	1.74 ± 0.40
	340	99.9	1.74 ± 0.53	316	100.0	1.71 ± 0.56

afternoon with only male *H. abdominalis* showing a decrease in these two patterns.

Prey selection.—Both species of *Holcocephala* selected similar prey taxa, with Diptera and Hymenoptera being taken most frequently (Table 4, see list of prey). Others (Dennis, 1979; Johnson, 1976; Bromley, 1950b; McAttee and Banks, 1920) have also reported that *Holcocephala* feed primarily on prey within these insect orders. *Holcocephala abdominalis* captured proportionally more hymenopterous and coleopterous prey and fewer homo-hemipterous and psocopterous prey than did *H. calva*. Both sexes of *H. abdominalis* captured prey in each taxa in almost equal proportions (Table 5). In contrast, female *H. calva* captured significantly larger proportions of hymenopterous, coleopterous, and homo-hemipterous prey and fewer dipterous and psocopterous prey than did conspecific males (Table 6).

Table 6. Dietary composition and characteristics of prey captured for *Holcocephala calva* in Maryland. Predator lengths (mm) 7.0 ± 0.52 ♂, $N = 20$; 7.48 ± 0.52 ♀, $N = 20$.

Prey	Females			Males		
	No.	%	\bar{x} SD	No.	%	\bar{x} SD
Diptera	96	26.2	2.08 ± 0.08^a	88	39.1	1.85 ± 0.73^a
Hymenoptera	119	32.4	2.52 ± 1.21^a	51	22.7	2.00 ± 1.02^a
Coleoptera	38	10.4	1.86 ± 0.62^b	21	9.3	1.90 ± 0.74^b
Homoptera, Hemiptera	64	17.4	1.85 ± 0.70^b	25	11.1	1.82 ± 0.87^b
Psocoptera	39	10.6	1.82 ± 0.54^b	33	14.7	1.81 ± 0.45^b
Misc.	11	3.0	1.89 ± 0.54	7	3.1	1.86 ± 0.31^b
	367	99.9	2.11 ± 0.92	225	100.0	1.89 ± 0.80

^a Significant difference within prey taxa between sexes at $P < .05$ level (*t* test).

^b No significant difference within prey taxa between sexes at $P < .05$ level (*t* test).

Larger asilids usually selected larger prey and vice versa (Table 4). Mean sizes for all prey taxa for *H. abdominalis* and *H. calva* were 1.73 and 1.95 mm, yielding predator-prey length ratios of 3.4 and 3.7, respectively. Most prey were less than 3 mm in length, with 96.3% and 87.2% for each species, respectively. Thus *H. abdominalis* captured significantly more ($Z = 4.53$, $P < .05$) small prey than did *H. calva*. Within the major prey taxa, only hymenopterous prey were not significantly different in size for the two species. The latter is the result of the proportionally large number of winged reproductive ants (70.4% *H. a.*; 34.1% *H. c.*) in each of the samples.

Females of *Holcocephala* were significantly larger than their conspecific males, and both sexes of *H. calva* were larger than those of *H. abdominalis* (Tables 5, 6). Sexes of *H. calva* usually selected larger prey within common taxa than did *H. abdominalis*. Furthermore, female *H. calva* selected larger dipteran and hymenopteran prey than did its conspecific male. Male *H. calva* captured primarily Apocrita Hymenoptera (98.9%), whereas females captured more formicids (48.1%). Removal of formicids from the females list reduced the mean hymenopteran size to 2.18 mm, which does not differ significantly from that of the male. Similar larger hymenopterous prey means for both sexes of *H. abdominalis* resulted from the large number of reproductive ants captured, and their removal produced similar results ($\bar{x} = 1.98$ mm). Comparisons of prey means within common taxa for the sexes of *H. abdominalis* show no significant difference in mean size.

The following are lists of prey taken by *H. abdominalis* and *H. calva* at the study site. In some instances prey are determined only to order or family level, since some prey were not taken or they were too damaged for identification. Each notation of prey refers to a single record unless followed by a number in parentheses. The month and year are recorded only once at the end of a series for each prey taken.

Prey of *H. abdominalis*.—ARANEIDA (all immatures): Agelenidae, unidentified 20 (2) 27.VIII.74; Clubionidae, Liocraninae 23.VIII.74; Thomisidae, Misumeninae 23.VIII.74; Salticidae unidentified (2) 28.VIII.74; Pisauridae, *Dolomedes* sp. 8.VIII.73. PSOCOPTERA: Unidentified 9.VIII.72; Ectopsocidae, *Ectopsocopsis cryptomeriae* (Enderlein) 22 (3) 27, 29.VIII.74, (9) 16.VIII.77, (6) 1, (2) 3.IX.77; Lepidopsocidae, *Echmepteryx hageni* (Packard) 22.VIII.74, 30.VIII.77; Psoquillidae, *Rhyopsocus* sp. 15.VIII.74. HOMOPTERA-HEMIPTERA: Aleyrodidae, unidentified 3.IX.77; Anthoridae, *Orius insidiosus* (Say) 9.VIII.72, 30.VIII, (3) 1.IX.77; Aphididae, unidentified (11) 28.VIII.74, *Anoecia corni* (F.) 16.VIII.74, *A. cornicola* Walsh 22.VIII.74, 16, (2) 30.VIII.77, *Aphis forbesi* Weed 22.VIII.74, *Chaitophorus pusillus* Hottes and Frison 25.VIII.74, *Macrosiphum* sp. 9.VIII.72, *M. liriodendri* (Monell) 22.VIII.74, (3) 16.VIII, (2) 1.IX.77, *Myzocallis* sp. 27.VIII.74, *Thecabius* sp. 22, 29.VIII.74; Cicadellidae, *Macrosteles fasciformis* (Stål) 11.VIII.72, nymphal Cicadellinae 27.VIII.74; Coccoidea, un-

identified 16.VIII, 3.IX.77; Delphacidae, *Delphacodes* sp. 28.VIII.74; Miridae, unidentified 25.VIII.74, (2) 28.VIII.75, *Halticus intermedius* Uhler (2) 3, 9.VIII.72. THYSANOPTERA: Phlaeothripidae, unidentified 9.VIII.72, 22, 23.VIII.74, 1.IX.77; COLEOPTERA: Chrysomelidae, *Chaetocnema* sp. 9.VIII.72, 23.VIII.74; Hydrophilidae, *Cryptopleurum minutum* Fabricius 7.VIII.72; Mycetophagidae, *Litargus tetraspilotus* LeConte 25.VIII.74, (12) 16.VIII, 3.IX.77; Orthoperidae, *Orthoperus* sp. (3) 16.IX.74; Phalacridae, *Olibrus* sp. 28.VIII.74; Ptilidae, *Actinopteryx* sp. (13) 27, (12) 23, (6) 22, 25, (5) 27, (3) 28, (2) 29.VIII.74, 16.IX.74; Rhizophagidae, *Monotoma longicollis* Gyllenhal 27.VIII.74; Scaphidiidae, *Eubaeocerus* sp. 23.VIII.74; Scolytidae, *Hypothenemus* sp. 29.VIII.74, 30.VIII, 1.IX.77, *Pityogenes hopkinsi* Swaine 20.VIII.74, *Pityophthorus pulicarius* (Zimmermann) 27.VIII.74, *P.* sp. near *puberulus* LeConte 27.VIII.74, *Xyleborus rubricollis* Eichhoff 27.VIII.74; Staphylinidae 22, (2) 23, (13) 27, (2) 28, 29, (3) 14, (6) 16, (4) 30.VIII.77. LEPIDOPTERA: Elachistidae, *Elachista* sp. 27.VIII.74. DIPTERA: Anthomyzidae, *Mumetopia occipitalis* Melander 9.VIII.72, 25.VIII.74, (2) 30.VIII.77, 1.IX.77; Cecidomyiidae, *Asteromyia* sp. 27, (13) 28.VIII.74, *Atrichopogon* sp. (2) 22, 25, 28, 29.VIII.74, 16, (2) 30.VIII.77, (13) 1.IX.77, *Cecidomyiidii* spp. (22) 22, 23.VIII.74, *Contarinia* sp. 28.VIII.74 (2) 16.VIII, (3) 3.IX.77, *Dasineura* sp. (2) 28.VIII.74, *Lestodiplosis* sp. (2) 27.VIII.74, *Lestremia* sp. (2) 28.VIII.74, *Micromya* sp. 27, 29.VIII.74, *Porricondyla* sp. 27.VIII.74, *Procystiphora* sp. 28.VIII.74, *Triopsis* sp. 27.VIII.74; Ceratopogonidae, *Dasyhelea* sp. 29.VIII.74, *Forcipomyia* sp. (7) 28.VIII.74; Chironomidae, Orthocladinae 29.VIII.74, *Cricotopus* sp. (2) 9.VIII.72, unidentified 22, 27, (16) 28.VIII.74, (13) 16, (4) 30.VIII.77, (3) 1.IX.77; Chloropidae, *Oscinella carbonaria* (Loew) 29.VIII.74, *O. umbrosa* (Loew) 9.VIII.72, 25.VIII.74, *Thaumatomyia bistriata* (Walker) 28.VIII.74; Dolichopodidae, *Chrysotus* sp. 9.VIII.72, 1.IX.77; Drosophilidae, *Drosophila melanogaster* Meigen (2) 9.VIII.72, (2) 30.VIII.77; Empididae, *Tachypeza* sp. 27.VIII.74; Ephydriidae, *Discocerina* sp. 9.VIII.72, *Hydrellia formosa* Loew (2) 22.VIII.74, *Leptopsilopa nigri-mana* (Williston) 28.VIII.74; Muscidae, *Coenosia* sp. 9.VIII.72; Phoridae, *Megaselia* sp. 20, (12) 28.VIII.74, (3) 16, 17, (2) 30.VIII.77, (3) 1.IX.77, *Puliciphora* sp. 20, (2) 28.VIII.74; Pipunculidae, *Chalarus spurius* (Fallén) 27.VIII.74; Psychodidae, *Psychoda* sp. 23.VIII.74; Scatopsidae, *Scatopse fuscipes* Meigen 28.VIII.74, 30.VIII.77; Sciaridae, *Bradysia* spp. (17) 22, (3) 23, (5) 25, (5) 27, (3) 28, (5) 29.VIII.74, *Sciara* sp. 15.VIII.74, (2) 30.VIII.77, (2) 1.IX.77; Sphaeroceridae, *Leptocera* sp. 28, (2) 29.VIII.74, *L. palliceps* Johnson 25, 28.VIII.74, 16.VIII.77, 3.IX.77. HYMENOPTERA: Unidentified (2) 27, (2) 28.VIII.74; Aphelinidae, unidentified 22.VIII.74; Aphidiidae, *Praon* sp. 23.VIII.74; Braconidae, *Aphaereta pallipes* (Say) 27.VIII.74, *Aspilota* sp. 20, 23, 28.VIII.74, *Chorebus* sp. 28.VIII.74, 12, 16.VIII.77; Ceraphronidae, *Ceraphron* sp. 20, 23.

29.VIII.74, *Dendrocerus* sp. 20, 23, 29.VIII.74; Cynipidae, *Hexacola* sp. 28.VIII.74, 16.VIII.77; Diapriidae, *Trichopria* sp. 28.VIII.74; Encyrtidae, unidentified 28.VIII.74, (4) 1.IX.77; Eulophidae, unidentified 22, 28.VIII.74, 12, (3) 16.VIII.77; Formicidae, *Ponera pennsylvanica* Buckley 28.VIII.72, 22, (13) 23, (22) 27, (12) 28, (17) 29.VIII.74, (16) 12.IX.74, (17) 16, (15) 30.VIII.77, (16) 1, (2) 3.IX.77, *Myrmecina americana* Emery (13) 22, 27, (3) 28.VIII.74, (6) 12, (2) 30.VIII.77; Mymaridae, unidentified 22, 28.VIII.74; Pteromalidae, 7.VIII.72, 20, 22, 28, 29.VIII.74, 30.VIII.77, 1, 3.IX.77; Scelionidae, *Gryon* sp. 27.VIII.74, *Telenomus* sp. 25, (3) 28.VIII.74.

Prey of *H. calva*.—ARANEIDA: Unidentified immatures 1.VIII.75, 9, 10, 12.VII.76, 1, 20, (3) 23.VII.77, 16.VIII.77; Linyphiidae, *Meioneta unimaculata* (Banks) 17.VII.74. PSOCOPTERA: Unidentified (2) 19.VIII.72, 12.VII.76; Caecilidae, *Caecilius aurantiacua* (Hagen) 30.VII.74, (2) 17.VII.75, (2) 10.VII.76; Ectopsocidae, *Ectopsocopsis cryptomeriae* (Enderlein) 1, (2) 16, (2) 22, (3) 29.VII.74, 20.VII.75, (2) 9, 10, (8) 12, (4) 13.VII.76, 1, (2) 20, 23.VII.77, 5, (3) 11, 15, (12) 16, (4) 22, (4) 25.VIII.77; Lepidopsocidae, *Echmepteryx hageni* (Packard) (3) 30.VII.74, 9.VII.76, 23.VII.77, (2) 16, 22.VIII.77; Philotarsidae, *Aaroniella* sp. 29, 30.VII.74, 12.VII.76. HOMOPTERA-HEMIPTERA: Aleyrodidae, unidentified 25.VIII.77; Anthocoridae, *Orius insidiosus* (Say) 22, (3) 25.VIII.77; Aphididae, *Anoecia graminis* G. and P. 1, *Aphis* sp. 30.VIII.74, *Chaitophorus pusillus* H. and F. 15.VIII.74, Drepanosiphinae (5) 9.VIII.72, *Myzocallis tiliae* (L.) 30.VIII.74, *Myzus* sp. 30.VIII.74, 25.VIII.77, *Prociphilus fraxinifolii* (Riley) 1.VIII.74, *Rhopalosiphum rufiabdominalis* (Sasaki) 30.VII.74, *Tinocalis ulmifolii* (Monell) (5) 30.VII.74, (2) 12, 15, (4) 30.VII.75, 1, (2) 5.VIII.75, (2) 1, (3) 9, (6) 15, (3) 16, (5) 20, 23.VII.77, 5, (5) 11, 15, (2) 16, (4) 22, (3) 25.VIII.77, unidentified 9, 10, 12.VIII.76; Cicadellidae, *Dikraneura* sp. (2) 27.VII.74, 9.VII.76, (2) 23, 11.VIII.77, *Scaphytopius* sp. 12.VII.76; Cixiidae, *Myndus pictifrons* Stål 16.VII.74; Delphacidae, *Delphacodes* sp. 16.VII.76, 25.VIII.77; Miridae, *Halticus intermedius* Uhler 9.II.72, 30.VII.74, 13.VII.76, 8.VIII.75, unidentified 20.VII.77, 16.VIII.77; Tingidae, *Corythuca ciliata* (Say) 12.VII.76. THYSANOPTERA: Unidentified 1, (2) 12.VIII.74, 5, 20.VII.77, 16, 22, 25.VIII.77. COLEOPTERA: Anobiidae, *Petalium* sp. 19.VIII.74; Chrysomelidae, *Chaetocnema* sp. 3.VIII.72, 30.VII.75, 13.VII.76, (2) 25.VIII.77; Ciidae, unidentified 29.VII.74, 23, (2) 16.VIII.77; Hydrophilidae, *Cercyon* sp. 6.VIII.75; Lathridiidae, *Aridius nodifer* (Westwood) 9.VIII.72, *Corticaria* sp. 30.VII.74, 9.VII.77, 11, (2) 16, 25.VIII.77; Mycetophagidae, *Litargus tetraspilotus* LeConte (2) 16, 22, (3) 25.VIII.77; Orthoperidae, unidentified 10.VII.76; Ptilidae, *Actinopteryx* sp. 10.VII.76; Staphylinidae, unidentified 29, (2) 30.VII.74, 1.VIII.74, 10, (4) 17, 22, 23, 29.VII.75, (5) 3.VIII.75, 10, (2) 12, 13.VII.76, 20.VII.77, (3) 23.VII.77, 5, (4) 16, (3) 22.VIII.77. LEPIDOPTERA: Tineidae, *Homosetia*

sp. 25.VIII.74. DIPTERA: Agromyzidae, *Phytomyza* sp. 16.VII.74, 13.VII.76, 16, (2) 22.VIII.77, *Cerodontha dorsalis* (Loew) 16.VII.74; Chironomidae, unidentified 15.VII.75, (12) 10.VII.76, (2) 5, 23.VII.77, 5, (4) 16, (3) 22, 25.VIII.77; Cecidomyiidae, *Lestremia* sp. 30.VII.75, 12.VII.76, 5, 13, (2) 20, 23.VII.77, 16, 22.VIII.77, *Lasioptera* sp. 9.VII.77, (2) 25.VIII.77; Ceratopogonidae, *Atrichopogon* sp. 12.VII.76, 5, 16, 22.VIII.77, *Forcipomyia* sp. 12.VII.76, (6) 16.VIII.77; Chloropidae, *Elachiptera erythropleura* Sabrosky (2) 22.VII.74, *Hippelates bishoppi* Sabrosky 22.VII.74, 1.VIII.74, 15.VIII.75, *Oscinella frit* (L.) 29.VII.74, (2) 22.VIII.77, *O. soror* (Macquart) 29.VII.74, 10.VII.76; Empididae, unidentified 22.VIII.77; Dolichopodidae, unidentified 13, 29.VII.75, 3.VIII.76, *Chrysotus* sp. 20, 23, 16.VIII.77; Mycetophilidae, unidentified 25.VIII.75; Phoridae, *Dohrniphora* sp. 30, (2) 9, (3) 12, 13.VII.76, 11, 15, (4) 16, 22.VIII.77, *Megaselia* sp. 30.VII.74, (3) 1.VIII.75, (4) 12, 13.VII.76, (2) 13, 15, 16, (4) 20, (4) 23.VII.77, 5, 16, 22.VIII.77, *Puliciphora* sp. (2) 30.VII.74, 9, 12.VII.76; Pipunculidae, *Tomosvaryella* sp. 25.VIII.77; Psychodidae, *Psychoda* sp. 25.VIII.77; Scatopsidae, *Scatopse fuscipes* Meigen 31.VII.75, 10, (2) 13.VII.76, 25.VIII.77; Sciaridae, *Bradysia* sp. 17.VII.74, (2) 29, (3) 30.VII.74, (3) 1.VIII.74, (2) 10.VIII.75, (2) 9, 10, (2) 13.VII.76, 1, (2) 5, (2) 9, (2) 13, 15, 16, (4) 20.VII.77, 5, (3) 11, (3) 15, (6) 16, (2) 23.VIII.77; Sphaeroceridae, *Leptocera* sp. 9.VII.72, (2) 12.VII.74, 15, 16, 20, (3) 23.VII.77, (5) 25.VIII.77; Stratiomyiidae, *Microchrysa polita* (L.) 19.VII.72. HYMENOPTERA: Unidentified (3) 17, (3) 22, (3) 29.VII.74, 1.VIII.74, (8) 26, (12) 29.VII.75, (5) 3, (6) 15.VIII.75; Aphidiidae, *Praon* sp. 30.VII.74; Braconidae, *Aphaereta* sp. 12, 9.VII.74, (3) 30.VII.75, 12.VII.76, 15, (2) 20.VII.77, (3) 5, 11.VIII.77, *Chorebus* sp. 30.VII.74, 9.VIII.74, 2.VII.75, *Euphoriella* sp. 30.VII.74; Cerafronidae, *Ceraphron* sp. 22.VII.74, *Dendrocerus* sp. 30.VII.74; Cynipidae, unidentified (3) 15.VIII.75, 12, 13.VII.76; Encyrtidae, unidentified 15, (2) 20, 23.VII.77, 5.VIII.77, (2) 16, 22, 23.VIII.77; Eupelmidae, unidentified (2) 20.VII.77; Eulophidae, unidentified 5, 16, 20, (5) 23.VII.77, 5.VIII.77, 11, 15, (3) 16, 22, 25.VIII.77; Formicidae, *Lasius* sp. (4) 26.VII.72, (3) 30.VII.74, 13.VII.77, *Myrmecina* sp. 5, 20.VII.77, (3) 11, 15, (3) 16.VIII.77, *Ponera pennsylvanica* Buckley (3) 30.VII.74, (10) 12, (7) 14, (8) 15.VIII.75, 9.VII.76, 13, 20, (3) 11, (4) 16, (3) 22.VIII.77; Perilampidae, unidentified 20.VII.77, 16, (7) 25.VIII.77; Pteromalidae, prob. *Habroclytus* sp. 9, (5) 12.VII.76, unidentified 15.VIII.77; Scelionidae, *Telenomus* sp. 30.VII.74, unidentified (2) 5.VIII.75.

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